TRACING SEA ICE ALGAE INTO VARIOUS BENTHIC FEEDING TYPES ON THE CHUKCHI SEA SHELF

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Abstract

Climate change in the Arctic is expected to have drastic effects on marine primary production sources by shifting ice-associated primary production to an overall greater contribution from pelagic primary production. This shift could influence the timing, amount, and quality of algal material reaching the benthos. We determined the contribution of sea ice particulate organic matter (iPOM) to benthic-feeding invertebrates by examining concentrations and stable carbon isotope values (expressed as $\delta^{13}C$ values) of three FAs prominent in diatoms: 16:4(n-1), 16:1(n-7) and 20:5(n-3). Our underlying assumption was that diatoms make up the majority in sea ice algal communities compared with phytoplankton communities. According to the FA concentrations, subsurface deposit feeders consumed the most iPOM and suspension feeders the least. Conversely, there were little differences in $\delta^{13}C$ values of FAs between deposit and suspension feeders, but the higher $\delta^{13}C$ values of 16:1(n-7) in omnivores indicated greater consumption of iPOM. We suggest that omnivores accumulate the ice algal FA biomarker from their benthic prey, which in turn may feed on ice algae from a deposited sediment pool. The dissimilar results between FA concentrations and isotope values suggest that the FAs used here may not be sufficiently source-specific and that other unaccounted for production sources, such as bacteria, may also contribute to the FA pool. We propose that FA isotope values are a more indicative biomarker than FA concentrations, but there is a further need for more specific ice algal biomarkers to resolve the question of ice algal contributions to the Arctic benthic food web.

Table of Contents **Page**

Abstract ..... **i**

List of Tables and Figures ..... **iii**

General Introduction ..... **v**

Chapter 1: Tracing sea ice algae into various benthic feeding types on the Chukchi Sea shelf **1**

Introduction **1**

Materials and methods **4**

Study region 4

Sample collection 4

Fatty acid analysis 5

Fatty acid-specific stable carbon isotope analysis 7

Data analysis 7

Results **8**

Fatty acid concentrations 8

Fatty acid stable carbon isotope values 9

Discussion **10**

Fatty acid sourcing based on concentrations 10

Tracing FA sources through stable isotope values 12

Spatial and temporal patterns in iPOM sourcing 14

Conclusions **15**

Acknowledgements **16**

General Conclusion **17**

Literature Cited **29**

List of Tables and Figures **Page**

Table 1 Coordinates of sampled stations with dates of sampling and respective program that sampled the station. Station numbers as in Fig. 1 19

Table 2 Stable carbon isotope values of the pPOM and iPOM for FAs 16:1(n-7), 16:4(n-1) and 20:5(n-3) for sampling in different years and data accumulated from different sources. Values are given as *means* in ‰ ± 1 *SD*. n/d indicates no data 20

Table 3 Overall *ANOVA* results for the comparison of FA concentrations with feeding type for 16:1(n-7), 16:4(n-1) and 20:5(n-3). Values are sum of squares (*SS*), mean squares (*MS*), degrees of freedom (*DF*), test statistics (*F*). * denotes significant differences at $\alpha = 0.05$, which was met at $p=0.0083$ after *Bonferroni adjustment* of the data 20

Table 4 *Tukey test with Bonferroni correction* for feeding type comparison for 16:1(n-7) and 16:4(n-1). * denotes significant differences at $\alpha = 0.05$, which was met at $p = 0.0083$ after correction 21

Table 5 Overall *ANOVA* results of comparison of FA isotope values with feeding type as factor for 16:1(n-7), 16:4(n-1) and 20:5(n-3). Values are sum of squares (*SS*), mean squares (*MS*), degrees of freedom (*DF*) and test statistics (*F*). * denotes significant differences at $\alpha = 0.05$ 21

Table 6 *Tukey test with Bonferroni correction* for feeding type comparison for 16:1(n-7). * denotes significant differences at $\alpha = 0.05$, which was met at $p = 0.0083$ after correction 22

Table 7 Linear regression analysis between FA stable carbon isotope values and sampling time for all feeding types for 16:1(n-7), 16:4(n-1) and 20:5(n-3). * denotes significant differences at $\alpha = 0.05$ 23

Table 8 Results of the 2-factor *ANOVA* with feeding type and station as factors for 16:1(n-7). Values are sum of squares (*SS*), mean squares (*MS*), degrees of freedom (*DF*) and test statistics (*F*). * denotes significant differences at $\alpha = 0.05$ 23

Fig. 1 Sampling stations (referred to by station #, see Table 1) in the Chukchi Sea in August and September 2012 with grey arrows denoting major water masses based on Pickart et al. (2010) 24

Fig. 2 FA concentrations for the FAs 16:1(n-7), 16:4(n-1) and 20:5(n-3) for different feeding types. Values are given as *means* ± 1 *SD* with different letters above bars denoting significant differences within each FA comparison. Note difference in y-axis scale for FA 16:4(n-1) 25

Fig. 3 $\delta^{13}C$ values (*mean* ± *SD*) for 16:1(n-7), 16:4(n-1), and 20:5(n-3) in relation to iPOM and pPOM $\delta^{13}C$ ranges with letters next to *SD* bars denoting significant differences. See Table 2 for iPOM and pPOM value origins 26

Fig. 4 $\delta^{13}C$ values for omnivores (A), subsurface deposit feeders (B) surface deposit feeders (C) and suspension feeders (D) over sampling time. Symbols represent FAs: 16:1(n-7) (black fill, continuous regression line), 16:4(n-1) (light grey fill, dashed regression line), 20:5(n-3) (no fill, dotted regression line). * denotes significant linear regressions at $\alpha = 0.05$ 27

Fig. 5 Spatial distribution of $\delta^{13}C$ values of 16:1(n-7) for all feeding types. Location of Wrangel Island as indicated in Fig.1 28

General Introduction

The Arctic has, in recent years, experienced the effects of climate change more so than other areas. This is true in particular for the effects of climate warming. Average water temperatures have continuously increased over the last decade with sea surface temperature anomalies having increased by 5 °C since 1995 (Steele et al. 2008). This increase in sea surface temperatures has contributed towards a decrease in sea-ice extent. The summer sea-ice extent has been declining at approximately 10-11 % per decade (Comiso et al. 2008; Perovich and Richter-Menge 2009). This change in sea-ice extent has also affected the onset of the melt season to be earlier and extended by 4-5 days (Markus et al. 2009). These changes and shifts have a tremendous effect on Arctic ecosystem functioning, starting with the timing, quantity and quality of primary production blooms. Ice algae are one such primary production source that can create large diatom blooms in early spring during the onset of sea ice melt (Campbell et al. 2009). Sea-ice algal communities are often diatom-based, especially common being pennate diatoms such as *Navicula* and *Nitzschia* (Gosselin et al. 1997; Kudoh et al. 1997), and establish within the brine channels of the sea ice. The taxonomic, chemical and biogeochemical composition of sea-ice algal communities is largely dependent on the physical and chemical properties of sea ice, such as thickness, brine channel volume, temperature, light availability, etc. (Gradinger 1999; Bluhm and Gradinger 2008). With a decrease in the length of sea ice-coverage overall as well as in sea-ice extent and thickness, sea-ice algal communities have less time to establish and may, in the future, produce much lower biomass (Horner 2017).

Given the effects of climate changes on the base of the food web, it is important to assess the possible consequences of changing quality, quantity and timing to consumers in the Arctic food web. Ice algal production is tightly coupled with benthic consumers (Wassmann and Reigstad 2011; Darnis et al. 2012). Benthic consumers capitalize on the early deposition of this material as well as on the high-quality food as sea-ice algae can contain a large amount of polyunsaturated fatty acids (Falk-Petersen et al. 1998). Tight links between benthic consumers and sea-ice algae (e.g., Kohlbach et al. 2016, Gaillard et al. 2017) could indicate dramatic consequences of shifts in sea ice algal production for benthic-dominated Arctic shelves. Detailed studies of the extent to which benthic organisms use sea-ice algal production are needed.

Chapter 1: Tracing sea ice algae into various benthic feeding types on the Chukchi Sea shelf[1]

Introduction

The seasonally ice-covered Chukchi Sea is one of the Arctic regions most likely to be affected by climate change, as evidenced by record low summer sea ice extent in 2007 and 2012 (Perovich and Richter-Menge 2009; Perovich et al. 2013). Changing sea ice phenology will likely influence the two main primary production sources in the Chukchi Sea: ice-associated and open water (Legendre et al. 1992; Tremblay et al. 2009). Sea-ice associated primary production occurs during the late-season sea ice cover in early spring when light levels and nutrient conditions are favorable. This sea-ice production occurs early enough in the season to escape zooplankton grazers, when their populations are not fully established within the water column (Springer et al. 1989; Carroll and Carroll 2003; Campbell et al. 2009). Much of the sea-ice particulate organic matter (iPOM) sinks to the sea floor in tight sympagic-benthic coupling where it supports the benthic food web (e.g., Grebmeier et al. 1988; Wassmann and Reigstad 2011). As the onset of sea ice melt becomes earlier and earlier in a warming Arctic, it will likely result in reduced iPOM as the growing season is reduced and ultimately, ice melt will start before the high light conditions needed for sea ice algal blooms are reached (Wassmann and Reigstad 2011). Sea-ice algae are considered a high-quality food for marine benthic consumers, as they are rich in essential polyunsaturated fatty acids (PUFAs; McMahon et al. 2006). Pelagic production, on the other hand, occurs later in the year under the high light and stratified water column conditions of late spring or early summer (e.g., Hunt et al. 2002). Although pelagic production can also produce larger amounts of PUFA (approximately 29 % versus 18 % in ice algae; Budge et al. 2008), pelagic production is consumed in greater proportion by pelagic grazers, which occur in high abundances in the water column at this time of year. Consequently, less net organic material from pelagic production reaches the sea floor communities during this later time (Wassmann and Reigstad 2011). Grazing of zooplankton in some regions has been reported to be 60% of the total primary production (Forest et al. 2008). The fraction of pelagic particulate organic matter (pPOM) that reaches the benthos is typically of lower quality, mostly in the form of broken cells, fecal pellets, and carcasses, after passing through the pelagic food web (Forest et al. 2008). This may result in benthic organisms preferentially using ice algae as a food source over phytoplankton (Sun et al. 2009), which, therefore, also may be the main contributors of PUFAs to the benthos. Other potential sources of primary production in the Arctic are microphytobenthos and under-ice blooms. Microphytobenthos, a diatom dominated community on the sediment surface (Wulff et al. 2009), is difficult to characterize for fatty acid and stable isotope composition because separating microphytobenthos from other organic matter sources such as detritus and microbes is very difficult (McTigue and Dunton 2014; Oxtoby et al. 2016). Under-ice blooms mostly seem to resemble pelagic phytoplankton communities but are very patchy in occurrence (Arrigo et al. 2012). Under current

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ice condition regimes, sea ice primary production in the Arctic ocean can account for 4-26% of the total annual primary production (Legendre et al. 1992; Tremblay et al. 2009), with approximately 5 % relative contribution of ice algal to total primary production reported in the Chukchi Sea (Gosselin et al. 1997). Although overall primary production in Arctic shelf regions is predicted to increase with a reduction or loss of sea ice due to increased light availability (Arrigo et al. 2008; Brown and Arrigo 2012), the amount of the early spring ice-associated primary production reaching the benthic communities will likely be greatly reduced (Arrigo et al. 2008).

Primary production from iPOM and pPOM settling to the seafloor builds much of the food base for benthic communities (e.g., Iken et al. 2010). The most common feeding types within the Arctic benthic macro-invertebrate community are omnivores (incl. predators/scavengers), subsurface deposit feeders, surface deposit feeders, and suspension feeders (Feder et al. 1994, 2005; Wlodarska-Kowalczuk et al. 2005; Pisareva et al. 2015). These feeding types occupy different trophic levels with omnivores and sub-surface deposit feeders typically at higher trophic levels compared with suspension and surface deposit feeders (Iken et al. 2010; Tu et al. 2015). We used a select number of benthic invertebrates to represent these different feeding types in the present study. One example of an omnivorous species from the Chukchi Sea is the snow crab, *Chionoecetes opilio*, which is abundant throughout the Chukchi Sea and can occasionally dominate the community in biomass and abundance (Feder et al. 2005; Bluhm et al. 2009; Ravelo et al. 2014). Snow crabs can directly consume primary production sources as detritus on the seafloor, but more often they feed on other invertebrates such as polychaetes, bivalves, and other crustaceans (Kolts et al. 2013; Divine et al. 2015). Suspension and deposit feeders are two of the most common feeding types of the Chukchi Sea benthos (Feder et al. 1994, 2007; Tu et al. 2015). Suspension feeders rely on suspended organic matter, consisting of either sinking fresh particles or re-suspended particles as a food source (Lopez and Levinton 1987). Surface deposit feeders ingest the top sediment layer consisting mostly of freshly deposited organic matter. Subsurface deposit feeders, in contrast, feed on less labile POM subducted into deeper sediment depths, often contributing substantially to bioturbation and reworking the top 5-10 cm of the substrate (Jumars and Wheatcroft 1989; Stead and Thompson 2006). Bivalves such as *Nuculana radiata* and *Macoma calcarea* are widespread examples of subsurface and surface deposit feeders, respectively, throughout the Chukchi Sea. They create important links between the primary production source and higher trophic level consumers such as benthic feeding birds and walrus (Bluhm and Gradinger 2008).

Understanding how possible changes in Arctic primary production will impact different benthic feeding types, and benthic communities in general, requires suitable biomarkers to trace the various production sources within the different feeding types. Ice algal communities mainly contain pennate diatoms, accounting for 70-99% of the total cell count (Booth and Horner 1997; Leu et al. 2010). A large proportion of ice algal communities is comprised of only a few very abundant species such as *Nitzschia frigida* and *Fragilariopsis* spp. (Horner and Schrader 1982; Booth and Horner 1997; Szymanski and Gradinger 2016). Phytoplankton communities, in contrast, can contain variable amounts of centric diatoms but also often also contain large proportions of flagellates

(Gosselin et al. 1997; Tremblay et al. 2009). Aside from these differences in overall taxonomic composition, fatty acid (FA) biomarkers can be used to trace primary production sources to invertebrate consumers in the marine environment (Oxtoby unpublished data; Wang et al. 2015). Three FAs, 16:4(n-1), 16:1(n-7) and 20:5(n-3), can be especially useful in tracing algal sources because as essential FAs they have to be taken up with the diet rather than synthesized *de novo* by the consumers (Dalsgaard et al. 2003; Iverson et al. 2004; Budge et al. 2011). Although all of the targeted FAs in this study can be produced by diatoms (Leu et al. 2010), some PUFAs, like 16:4(n-1), are considered the most specific marker for diatom origin, and with that may be an especially good biomarker of iPOM origin as compared with pPOM (Dalsgard et al. 2003; Parrish 2013). Other PUFAs such as 20:5(n-3) (eicosapentaenoic acid) also are predominantly produced by primary producers in the marine environment (Bajpai and Bajpai 1993) but can also be synthesized from other FAs by some organisms such as fish (Bell et al. 1986). However, uptake of this FA through diet is more efficient than synthesizing it from other FAs (Bajpai and Bajpai 1993; Bergé and Barnathan 2005), making it still a reliable marker of photosynthetic production. Monounsaturated FAs (MUFAs) like 16:1(n-7) are largely produced by diatoms but can, in some cases, have a bacterial origin as well (Kelly and Scheibling 2012; Parrish 2013). MUFAs such as 16:1(n-7) can account for 40% of the FA composition in ice algae (McMahon et al. 2006). In some extreme instances, 16:1(n-7) alone can account for 50% of FA composition in ice algae (Budge et al. 2008). The high prevalence of this FA in ice algae makes it a useful biomarker of ice algal FA sources in benthic consumers.

To more accurately specify the sources of FAs in benthic consumers, we pair FA concentrations with FA stable carbon isotope values (expressed as $\delta^{13}C$ values). Since sea ice brine channels have limited exchange with the outside medium, the naturally more abundant and metabolically preferred ^{12}C photosynthetic substrates (CO_2 and HCO_3^-) become depleted at high ice algal production rates such as during blooms (Thomas and Papadimitriou 2003). This results in an increased use of photosynthetic substrates with the heavier carbon isotope (^{13}C); consequently, FAs produced within sea ice algae become enriched in ^{13}C compared with material produced in the water column (Wang et al. 2014). For example, 20:5(n-3) from ice algae has reported $\delta^{13}C$ values of -21.9 ‰ compared with -32.0 ‰ in phytoplankton (McMahon et al. 2006). The isotopic signature of the essential FAs taken up through diet is conserved and can be traced in consumers to identify FA sources (e.g., Wang et al. 2015).

Assessing how benthic consumers are linked to iPOM is important to better understand potential change in energy flow through the Arctic ecosystem under expected climate change scenarios. Our objective was to determine the proportional contribution of iPOM relative to pPOM to different benthic feeding types, represented by a select number of benthic invertebrate consumers, in the Chukchi Sea. Given the rich history of using fatty acid concentrations to identify trophic linkages (Daalsgard et al. 2003; Kelly and Scheibling 2012; Gaillard et al. 2017) we aimed here to compare results from FA biomarker concentrations with $\delta^{13}C$ values from analyses of the same three FAs as the likely more specific biomarker approach to identify iPOM versus pPOM sources. We tested three hypotheses: (1) Suspension feeders consume the highest proportion of diatoms, presumably deriving mostly from

ice algae, among all feeding types as evidenced by highest concentrations in the most diatom-specific FA 16:4(n-1). This is based on our assumption that iPOM has a higher contribution fo diatoms than pPOM. (2) Suspension feeders consume fresh algal material such as from ice algae compared with other feeding types, resulting in target FAs that are enriched in ^{13}C. Using the isotope values of FAs as a second biomarker approach, this will test if suspension feeders indeed feed more on ice algae as stated in hypothesis 1. (3) Consumers sampled at later dates have higher FA $\delta^{13}C$ values than those sampled earlier in the season, due to the longer time consumers had to consume and assimilate ice algal material.

Materials and methods

Study region

This study was conducted on the Arctic Chukchi Sea shelf ranging from 66°N to 73°N and 161°W to 179°W (Figure 1). The Chukchi Sea is an inflow shelf with an average depth of about 50 m and seasonal ice cover (Woodgate et al. 2005). In the Chukchi Sea, freeze up occurs generally in late September, while the melt season typically starts late May (Belchansky et al. 2004; Markus et al. 2009). The Chukchi Sea is influenced by different water masses entering through the Bering Strait, including the relatively warm, freshwater-influenced and nutrient-poor Alaska Coastal Water, which travels north on the eastern margin and then partially turns east into the Beaufort Sea. Bering Shelf Water and the nutrient-rich Anadyr Water also flow north through the Bering Strait, where they largely mix to form the colder Bering Sea Anadyr Water (Weingartner et al. 2005; Pickart et al. 2010). This water mass branches into a northward flow following the Central Channel towards Hanna Shoal and a western branch flowing north on the Russian part of the shelf to drain through Herald Canyon (Weingartner et al. 2005). Local water masses in the northeastern Chukchi Sea include Winter Water formed during sea ice freeze up, which can persist on the bottom of the shelf even into the summer. During spring and summer, sea ice melt forms a fresh surface meltwater layer that aids in the stratification of the water column. Different water masses carry differing nutrient loads that can affect local primary production in sea ice and water column in the Chukchi Sea, with the respective quantity of these two primary production sources depending on seasonal sea ice cover (Walsh et al. 1989; Hansell et al. 1993).

Sample collection

Crabs and clams, as representatives of various common benthic feeding types, were collected at 14 stations on the Chukchi Sea shelf in August and September 2012 during the Russian-American Long-term Census of the Arctic (RUSALCA), the Chukchi Sea Offshore Monitoring In Drilling Area (COMIDA), and the Arctic Ecosystem Integrated

Survey (Arctic Eis) cruises (Figure 1, Table 1). All samples were collected using bottom trawls or van Veen grabs at depths ranging from 34-57 m. Samples included omnivores (the crab *Chionoecetes opilio*; Kolts et al. 2013; Divine et al. 2015), subsurface deposit feeders (the bivalve *Nuculana radiata*; Weems et al. 2012), surface deposit feeders (the bivalves *Macoma* spp. and *Ennucula tenuis*; McMahon et al. 2006; Weslawski et al. 2012), and suspension feeders (the bivalves *Liocyma fluctuosa*, *Serripes groenlandica*, and *Astarte* spp.; McMahon et al. 2006; Petersen and Curtis 1980). Thus, while feeding types are represented only by a few species, these taxa are very abundant on the Chukchi Sea shelf (e.g., Grebmeier et al. 1989; Bluhm et al. 2009; Blanchard et al. 2013) and are being used here in the larger context of the feeding types they represent. Species were collected in replicates of four at each sampling station, where possible, totaling 155 samples. All organisms were measured for shell length or carapace width. Organisms were kept frozen at -20°C before freeze-drying in a Virtis Freeze Dryer (model 52; The Virtis Company, NY, USA). Bivalve soft tissue was removed from the shell prior to freeze-drying, while *C. opilio* were freeze-dried whole. Freeze-dried samples were homogenized and stored in crimp top vials under nitrogen atmosphere at -80°C until lipid extraction. All wet and freeze-dried tissue weights were taken on a Mettler Toledo AX205 analytical balance (Greifensee, Switzerland) to the nearest 0.0001 g.

In addition to organism samples, ice algal samples were collected at nine stations in May and June 2014 during the Study of Under-ice Blooms in the Chukchi Ecosystem (SUBICE). No ice samples were taken during the invertebrate collection cruises because those occurred during the open water season. The bottom 10 cm of three ice cores (9 cm diameter) per station were melted in pre-filtered seawater in darkness to reduce osmotic stress for algal cells (Bates and Cota 1986). Ice algae were then filtered onto pre-combusted Whatman GF/F glass fiber filters. Ice algal filters were stored at -20°C in small petri dishes, wrapped with Parafilm® M for airtight storage, until lipid extraction and isotope measurements. One filter per station was analyzed for iPOM carbon isotope values. PPOM collections did not yield sufficient material for successful fatty acid extraction.

Fatty acid analysis

One subsample per individual sample was analyzed, and sample replication was obtained from analyzing multiple individuals per feeding type. A 0.5 g homogenized, freeze-dried tissue sub-sample per organism, or less if less material was available (smallest sample was 0.0144 g), was added to approximately 0.5 g hydromatrix (Dionex, CA, USA) and thoroughly mixed. The mixture was then placed into an 11 ml stainless steel thimble prepared with two cellulose filters and a thin layer of sand. After adding another cellulose filter to the top of the thimble, it was loaded into an accelerated solvent extraction (ASE) system (Dionex ASE 200, CA, USA). Lipids were extracted with two static cycles (5 min each), utilizing dichloromethane (DCM; Fisher Thermo-scientific, Fair Lawn, NJ, USA) as the solvent system at 85°C under 1500 psi nitrogen. Butylated hydroxytoluene (BHT; Sigma Chemical, St. Louis, MO, USA) was added to the DCM at a concentration of 100 mg/L to prevent lipid oxidation.

Ice algal filters were extracted in centrifuge tubes with 2 ml chloroform and 1 ml ice-cold methanol (Folch et al. 1957; Parrish 1999). Filters were then ground to a pulp with a glass rod, sonicated and centrifuged. The organic layer was removed and kept, and the remaining filtrate was re-extracted three more times with 1 ml chloroform each. The organic phases of all extractions of a sample were pooled to yield the total lipid extract.

Lipid extracts were concentrated at 36°C under nitrogen atmosphere using a solvent evaporation system (TurboVap, Zymark INC, Hopkinton, MA, USA). Solvent-free lipid extracts were weighed to determine percent lipid per dry weight sample. Lipids were then transformed into fatty acid methyl esters (FAMEs) according to Iverson et al. (2002), using an acid-catalyzed esterification process. An internal standard, methyl tricosanoate (23:0; Sigma Aldrich, Saint Louis, MO, USA), was added at the beginning of this procedure at 1 mg/20 mg lipid samples (proportionally less for smaller sample sizes). The internal standard allowed for later quantification of sample FAs by direct comparison of the area under the curve in the gas chromatography output. Solvent was completely removed from the esterified lipids, using the TurboVap, and the extracts were diluted in hexane to a concentration of 20 mg/ml. FAMEs are described here by the A:B(n-X) nomenclature, where A is representative of the number of carbon atoms, B the number of double bonds, and X the position of the closest double bond to the terminal methyl group. The three target FAs, 16:4 (n-1), 16:1(n-7) and 20:5(n-3), were identified by comparing peak retention times in gas chromatography (GC-FID, model 6850, Agilent Technologies, Wilmington, DE) profiles to known fatty acid standards (18919-1AMP Supelco; Sigma Aldrich, Saint Louis, MO, USA). This standard was used to create calibration curves with a range of FAME concentration from 0.1 to 1.0 mg for quantification of 16:1(n-7) and 20:5(n-3). We use FA concentrations rather than proportions because it results in higher accuracy when only focusing on three FAs. FA peaks were only integrated for the targeted FAs; therefore, target FA proportions would be calculated based on this total peak area, not reflecting true proportions with regards to total FA content. Calibration curves for both FAs were extended to 5 mg/ml, utilizing analytical standards for 20:5(n-3) (47571-U; Sigma Aldrich, Saint Louis, MO, USA) and 16:1(n-7) (02156048; MP Biomedicals, Santa Ana, CA, USA), to cover the FAME concentration ranges found in samples. The identity of 16:4(n-1) and its exact retention time were confirmed by the use of the PUFA-3 standard (1177, Matreya LLC, State Collega, PA, USA). The Calibration curve of the FAME of 18:4(n-3) (10005000, Cayman Chemical, Ann Arbor, MI, USA) was used to quantify 16:4(n-1), for which no pure commercial standard is available. Ackman response factors were applied to correct FA areas of the calibration curve (Ackman and Sipos 1964) because the areas are not identical for the same quantity of different FAs due to slightly distinct molecular ionization processes, which result in different responses by the flame ionization detector (FID) of the GC. To correct for this variability, the FAME of 18:0 is commonly used as a baseline reference because it is in the middle of the chromatogram of most marine lipid samples and thus a good overall representative (Ackman and Sipos 1964). The Ackman response factor is the recorded area of the calibration curve divided by the FAME of 18:0 area value. Corrected FAME areas were then related back to the area of the internal standard methyl tricosanoate (23:0), which has a known quantity associated with its area. FAME concentrations were reported as mg FA/mg lipid.

Fatty acid-specific stable carbon isotope analysis

The carbon stable isotope ratios ($^{13}C/^{12}C$) of individual FAMEs in FAME samples were measured once for each organism using continuous-flow isotope ratio mass spectrometry (IRMS, Thermo Finnigan Delta V) at the Alaska Stable Isotope Facility, University of Alaska Fairbanks. Stable isotope ratios are reported in the conventional δ notation as ‰ deviation from the international standard VPDB (Vienna Pee Dee Belemnite), according to the following equation:

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] * 1000$$

where R is the corresponding ratio $^{13}C/^{12}C$. Previous studies analyzing $\delta^{13}C$ values of FAMEs have corrected ratios for the additional methyl group added during the esterification procedure (Budge et al. 2008; Bec et al. 2011; Wang et al. 2014). This correction was not done here because the isotope difference entirely depends on the carbon chain length of the fatty acid (Wang et al. 2014). Because the three FAs targeted here have very similar chain lengths, this isotopic difference is negligible (Abrajano et al. 1994). To ensure analytical precision, a crab tissue extract was used as a working standard and calibrated against an isotopic standard containing eight n-alkanoic acid esters (F8 Mixture, Indiana University Stable Isotope Reference Materials). The crab standard was a large freeze-dried and homogenized snow crab that was not included as a sample in this study. Five subsamples of the homogenate were FA extracted and FAME derivatized. These five crab standard subsamples and the F8 Mixture were run ten times to test the consistency of the $\delta^{13}C$ values within multiple crab subsamples. On average, the n-alkanoic acid esters had a standard deviation of 0.2 ‰ from their respective means. The $\delta^{13}C$ values in the five crab standard subsamples were -24.8 to -24.4 ‰ (mean -24.6 ($\pm$ 0.4) ‰) for 16:1(n-7) and -26.9 to -26.4 ‰ (mean -26.6 ($\pm$ 0.9) ‰) for 20:5(n-3). The FA 16:4(n-1) was present in insufficient quantity to be detected with accuracy. The crab standard was then run intermittently after every ten samples.

Data analysis

Benthic taxa were analyzed according to their feeding strategy as omnivores, subsurface deposit feeders, surface deposit feeders, and suspension feeders. FA concentrations as well as FA $\delta^{13}C$ values were compared among feeding types by fitting a linear model using the lme4-package and by analysis of variance (ANOVA) with the lmer test-package in the software program R (R v3.1.3). A separate *Tukey post-hoc test* with *Bonferroni correction* was

applied if feeding type was a significant factor, maintaining a significance level α=0.05 at p-values $\leq$ 0.0083. Additionally, where feeding type was a significant factor in FA carbon stable isotope analysis, a 2-factor *ANOVA* with feeding type and sampling station as factors was applied. Linear regression analyses were used to determine whether a temporal trend existed between sampling date and FA $\delta^{13}C$ values for the different feeding types (R v3.1.3). Significance level for all analyses was set at α=0.05.

FA concentrations and $\delta^{13}C$ values were correlated with environmental variables to determine the best predictors, using multivariate analyses (Primer-E v7). Environmental variables included latitude, longitude, depth, bottom temperature, and bottom salinity. FA concentrations were normalized in Primer-E to bring all measurements to a similar scale (16:4(n-1) occurred at an order of magnitude lower concentration than 16:1(n-7) and 20:5(n-3)) and all concentration data were then log (X+1) transformed. The FA $\delta^{13}C$ values were square-root transformed for multivariate analyses. A resemblance matrix based on Euclidean distances was created for both FA concentrations and FA $\delta^{13}C$ values; both were used in *BEST-BioEnv* analyses to determine which normalized environmental variables correlated best with the FA concentration and FA $\delta^{13}C$ data (Spearman Rank correlations).

Reference data for FA $\delta^{13}C$ values from iPOM and pPOM to determine source contributions to the different feeding types were taken from a variety of seasonal conditions: 2014 samples from the Chukchi Sea collected during ice melt in May/June (analyses from this study, iPOM only); 2010 data collected during maximum ice extent (March), ice melt (May/June) and ice free (June) conditions in the Bering Sea (Wang et al. 2014); 2009 data collected during ice melt in April/May in the Bering Sea (Wang et al. 2014); and 2002 data collected during ice melt in May off of Barrow, Alaska (Budge et al. 2008, Table 2). The Bering Sea 2014, 2010 and 2009 iPOM samples were collected from melted bottom ice cores, while pPOM samples were collected via Niskin bottles attached to a CTD rosette (Wang et al. 2014). PPOM in 2002 off Barrow was collected from water samples from approximately 5 m under the ice, while iPOM samples obtained from bottom sea ice cores (Budge et al. 2008). All samples were filtered onto GF filters.

Results

Fatty acid concentrations

Mean (± *standard error*) total FA concentrations were lowest in omnivores (5.9 ± 0.9 %), followed by suspension feeders (7.0 ± 0.6 %) and surface deposit feeders (9.0 ± 1.0 %), and were highest for subsurface deposit feeders (15.5 ± 2.6 %). Concentrations of the three focal FAs differed greatly in all feeding types, with the abundances of 16:4(n-1) being an order of magnitude lower than those of 16:1(n-7) and 20:5(n-3) for all feeding types. For example, across feeding types 16:1(n-7) had the highest average concentration at 0.19 ± 0.1 mg FA/mg lipid, while

the concentration of 16:4(n-1) was much lower at 0.01 ± 0.001 mg FA/mg lipid. Differences in individual FA concentrations among feeding types were greatest for 16:1(n-7), with the lowest mean values in omnivores (0.11 mg FA/mg lipid) and the highest in subsurface deposit feeders (0.26 mg FA/mg lipid; Figure 2). The FA concentrations of 16:1(n-7) and 16:4(n-1) were highest in subsurface deposit feeders, followed by surface deposit feeders, suspension feeders, and were lowest in omnivores (Figure 2). Both FAs were significantly higher in subsurface deposit feeders than in omnivores and suspension feeders (ANOVA, Table 3; *Tukey test with Bonferroni correction*, Table 4). No differences in FA concentrations among feeding types were found for 20:5(n-3) (Table 3, Figure 2). The environmental variables tested (latitude, longitude, depth, bottom salinity, bottom temperature) did not explain a significant amount of the variation found in FA concentrations.

Fatty acid stable carbon isotope values

Across all feeding types, $\delta^{13}C$ values (*mean* ± *SD*) were lowest in 16:4(n-1) (-31.66 ± 2.29 ‰) and highest in 16:1(n-7) (-26.89 ± 2.09 ‰), with a 5 ‰ difference between the FA means. Consistent with the patterns in FA concentrations, 20:5(n-3) $\delta^{13}C$ values were not significantly different among feeding types (Table 5). In contrast to FA concentrations however, feeding type only was a significant factor for 16:1(n-7) but not for 16:4(n-1) $\delta^{13}C$ values (Table 5). Omnivores had significantly higher 16:1(n-7) $\delta^{13}C$ values compared with suspension feeders (Figure 3, Table 6).

The combination of environmental variables latitude, longitude, and bottom salinity was the strongest predictor of FA $\delta^{13}C$ values, albeit at low explanatory power (*BEST-BioEnv*, $\rho = 0.234$). Over the sampling period, $\delta^{13}C$ values of 16:1(n-7) significantly increased (by 1.58 ‰ and 4.63 ‰) in surface deposit feeders and suspension feeders, respectively, and significantly decreased (by 7.89 ‰) in omnivores (Figure 4, Table 7). The 16:4(n-1) $\delta^{13}C$ values increased significantly over the sampling period in omnivores and surface deposit feeders (by 3.16 ‰ and 2.52 ‰, respectively), and 20:5(n-3) $\delta^{13}C$ values increased significantly in all feeding types (suspension feeders: 4.63 ‰, surface deposit feeders: 2.79 ‰ and subsurface deposit feeders: 2.60 ‰) except omnivores (Figure 4, Table 7). However, temporal trends were weak for all FA $\delta^{13}C$ values over the 41-day sampling period despite statistical significance (Table 7, Figure 4).

Considering the significant difference in $\delta^{13}C$ values of 16:1(n-7) among feeding types (Figure 3), we explored the effect of sampling location on the $\delta^{13}C$ values of this FA (2-factor *ANOVA*, Table 8). Feeding type, station, and the interaction between both factors were significant (Table 8). Omnivores had the largest spatial differences in 16:1(n-7) $\delta^{13}C$ values (Figure 5), with higher values at northern stations (north of 68°N) than at more southern stations (south of 68°N); $\delta^{13}C$ values near Wrangel Island were highest. Subsurface deposit feeders had, overall, a much lower range in 16:1(n-7) $\delta^{13}C$ values and no clear spatial patterns were discernable, but only two

stations were sampled for this feeding type in the southern region. The opposite trend occurred in $\delta^{13}C$ of 16:1(n-7) in surface deposit feeders and suspension feeders, which were the lowest in the northwestern Chukchi Sea and had the highest $\delta^{13}C$ values in the southern region (Figure 5). However, additional analyses with respect to regional groupings of stations or length of sea ice cover at the sampling stations did not reveal any spatial patterns in FA $\delta^{13}C$ values within feeding types (data not shown).

Ice algal FA $\delta^{13}C$ values from the literature and our own measurements were highly variable while literature FA $\delta^{13}C$ values for pPOM had a much narrower range (Table 2, Figure 3). The range of $\delta^{13}C$ values of 16:1(n-7) in omnivores overlapped most with the iPOM $\delta^{13}C$ range, followed by subsurface deposit feeders, surface deposit feeders and little overlap in suspension feeders (Figure 3). None of the $\delta^{13}C$ values for 16:4(n-1) in any of the feeding types overlapped with the iPOM source (Figure 3). 20:5(n-3) isotope values also overlapped only with iPOM source values by Wang et al. (2014) for all feeding types, while there is considerable overlap with all pPOM values (Figure 3).

Discussion

The goal of this study was to determine the contribution of iPOM to the diet of various benthic feeding types, based on three FAs used as biomarkers of ice algal production. We found that, based on FA concentrations, subsurface deposit feeders sourced the highest quantity of FAs from iPOM, while the relatively high $\delta^{13}C$ values of 16:1(n-7) indicated that omnivores consumed the most iPOM. Here, we consider various explanations for these differing results in the two biomarker approaches, such as FA specificity in production sources, the possibility of a bacterial origin of the FAs, as well as the accumulation of iPOM in a 'food bank' as a long-term food source for benthic consumers.

Fatty acid sourcing based on concentrations

The two main primary producer food sources for benthic consumers in the Arctic, either of ice-associated or pelagic origin, often are characterized by different dominant taxonomic groups. Different taxonomic groups have different FA profiles that can be used as biomarkers (Dalsgaard et al. 2003). In general, good biomarkers are source specific and preserved through the food web and over time, making them possible to track across trophic connections (Dethier et al. 2013). Of the three FAs under investigation in this study, 20:5(n-3) has the most ubiquitous sources, including a variety of primary producers as well as protozoans, and it can even be synthesized by some higher trophic levels (Bajpai and Bajpai 1993; Schmidt et al. 2006; Kelly and Scheibling 2012; Parrish 2013). This essential FA is important for growth and reproduction in all marine organisms (Hendriks et al. 2003)

and occurs in great abundance in most marine organisms (Bergé and Barnathan 2005). This could explain why its concentrations did not vary significantly among feeding types and suggests that 20:5(n-3) concentration may not be an ideal biomarker to distinguish between ice algal and phytoplankton sources.

We expected suspension feeders to have the highest concentration of the most diatom-specific FA 16:4(n-1) because suspension feeders consume large amounts of the fresh algal material settling from the water column, including sea ice algal diatoms. Instead, suspension feeders had lower 16:4(n-1) concentrations than subsurface and surface deposit feeders, although the difference was only significant for subsurface deposit feeders. Benthic suspension feeders feed on algal material while it is suspended during the time of sinking to the bottom or when it becomes re-suspended from near-bottom flow (Farrow et al. 1983; Wegner et al. 2003). The time when suspended algal cells are within abundant reach of the feeding apparati of the benthic suspension feeders is likely much shorter than for subsurface and surface deposit feeders, which can consume the algal material after it has settled onto the benthos, perhaps extending the duration during which they can access iPOM. Additionally, subsurface and surface deposit feeders may be feeding on algal material or FAs stored in the sediment from previous years. Although PUFA generally degrade quickly, PUFA have been found to persist at depths below 5000 m as well as being preserved long-term in sediments (DeBaar et al. 1983; Budge and Parrish 1998). Studies in the Antarctic have addressed the idea of the sediment serving as a food bank in which organic matter from past blooms is stored (Mincks et al. 2005; Glover et al. 2008), and such a food bank has been proposed as a food source for Arctic bivalves as well (Weems et al. 2012). Although we do not have fatty acid concentration measurements of the sediment, such sedimentary food storage could provide the various deposit feeders with longer-term access to ice algal material than for suspension feeders, if indeed a large amount of the ice algal bloom is deposited and not consumed while suspended. Export production in the Chukchi Sea can range from 3-47 g $C/m^2/d$ during seasonal production peaks depending on location, and a substantial amount of this carbon is not readily consumed and is retained in shelf sediments (values published by Grebmeier et al. 2006 were adjusted to a per day scale). At higher trophic levels such as omnivores, the FA composition is likely less derived from direct consumption on primary producers but may rather reflect the food sources of their prey organisms, which in turn have consumed the primary production (Iverson 2009). While this ultimately describes the reliance of these higher trophic levels on specific energy pathways, the reliance on a specific primary production source is indirect and buffered through multiple trophic steps.

The FA concentration data indicate that subsurface deposit feeders consume the most diatoms, potentially ice algae, with suspension feeders consuming the least. However, post-consumption metabolic processes and physiological requirements may process FAs from diet differently in the different feeding types, and concentration of a FA alone may not directly relate to a source. In addition, with some of the target FAs not being exclusive to a specific source and/or some producer overlap (diatoms) between the sea ice and pelagic

environments, an additional biomarker is needed to elucidate the specific sourcing of these FAs. We employed FA specific stable carbon isotope analysis as such a tool.

Tracing FA sources through stable isotope values

Stable carbon isotope values have previously been used to trace sea ice-derived production through the Arctic food web (e.g., Søreide et al. 2006; Weems et al. 2012). Similar to FA concentrations, $\delta^{13}C$ values of 20:5(n-3) did not display any differences among feeding types and indicated that neither feeding type strongly sourced this FA from iPOM. The 20:5(n-3) produced in iPOM samples is typically more enriched in ^{13}C than in pPOM; however, the $\delta^{13}C$ values of this FA from the two primary production sources can vary between years (Wang et al. 2014). The $\delta^{13}C$ values of 20:5(n-3) in pPOM are fairly constant throughout the year, but the $\delta^{13}C$ values of 20:5(n-3) in iPOM are higher later in the season during ice melt compared with maximum ice extent, when values are more similar to pPOM values. This seasonal difference in $\delta^{13}C$ values of 20:5(n-3) in iPOM makes it difficult to distinguish between iPOM and pPOM origin in consumers. Additionally, 20:5(n-3) is one of the few PUFAs that can also be produced by bacteria in low temperature environments to maintain cell membrane fluidity (DeLong and Yayanos 1986; Bajpai and Bajpai 1993; Shulse and Allen 2011), adding an additional source of this FA. This makes 20:5(n-3) more ubiquitous and is likely a reason why there was no distinction between the feeding types in our study. Therefore, this FA is likely not a sufficiently specific biomarker for ice algal consumption.

The $\delta^{13}C$ values of 16:4(n-1) strongly overlapped with the pPOM source for all consumer types, although results on FA concentrations of 16:4(n-1) had suggested that subsurface and surface deposit feeders consumed more iPOM. In contrast, subsurface deposit feeders had the lowest $\delta^{13}C$ values in 16:4(n-1), suggesting comparatively lowest iPOM consumption, although differences were not significant. This difference between FA isotope and concentration results for 16:4(n-1) could be due to the very low concentrations of this FA in the organisms' diet. At low concentrations, analytical errors may be close to biological variability or differences among feeding groups; similarly, $\delta^{13}C$ values may be more susceptible to variation in the carbon kinetic isotope effect in FA synthesis at low FA concentrations (e.g., Monson and Hayes 1982). Alternatively, or in addition, a different and unknown primary production origin of 16:4(n-1) could impact the isotope results. Our current knowledge is that this FA is primarily produced by diatoms and is otherwise only found in trace amounts in dinoflagellates, coccolithophores and other microalgal groups (Dalsgaard et al. 2003). These trace sources might become influential when the FA only occurs overall at low concentrations. Another explanation for the differences found between isotope and concentration results for 16:4(n-1) could be unknown metabolic processes after consumption in different feeding types or unknown FA turnover rates. Turnover refers to the time it takes to replace stable isotopes in tissues or molecules (like FAs) with the stable isotope values from a new diet (Tieszen et al. 1983; Hobson and Clark 1992). Isotope turnover rates could obscure FA isotope differences between feeding

types because turnover rates are influenced among others by the concentration of a FA (Budge et al. 2011; Hückstädt et al. 2012). The timing differs when the iPOM and pPOM sources become available to the feeding types, and thus, how long they had to feed on these sources and isotopic turnover to take place at the time of sampling. The ice algal bloom in the Arctic generally occurs between March and May (Brown et al. 2011), with the phytoplankton bloom occurring as early as May/ June, depending on ice conditions (Arrigo et al. 2008). This means that the phytoplankton bloom was approximately 1-2 months closer to the timing of our organism collection (August/September) than the ice algal bloom. Isotopic turnover rates in Arctic bivalves are similar regardless of the feeding type (McMahon et al. 2006) and only change 1-2‰ every 2-3 weeks when fed a highly isotopically enriched food source, until equilibrated to the enriched source (Weems et al. 2012). Therefore, we would assume that these consumers could still show a strong ice algal signal at the time of collection if they had been feeding on iPOM before pPOM became available, unless they have a much faster turnover time than established in previous studies. If this were the case, our late sampling could pick up the isotope signal from the pPOM pulse being incorporated into the organisms' tissue, overriding any previous iPOM enriched values.

The relatively high $\delta^{13}C$ values from analyses of 16:1(n-7) in omnivores indicate that, directly or indirectly, omnivores consume the most ice algal-derived material of all feeding types. Although the potential bacterial origin of this FA also has to be acknowledged (Kelly and Scheibling 2012; Parrish 2013), high concentrations of this FA originate mostly from diatoms rather than bacteria (Dalsgaard et al. 2003). In sea ice diatoms, MUFA production, particularly 16:1(n-7), increases over time because of the increase in light availability later in the season, while other FAs have a more continuous production rate (Leu et al. 2010). The growth rate and standing stock of sea ice diatoms are also increased later in the season, adding pressure to the dissolved inorganic carbon pool and decreasing discrimination between carbon isotopes (Fischer 1991), thus increasing $\delta^{13}C$ values of MUFAs. With increased production of 16:1(n-7) (Kohlbach et al. 2016), decreased carbon discrimination could particularly affect the isotope values of this FA. Under these late season conditions, large quantities of isotopically heavy 16:1(n-7) may be channeled into the benthic food web. These isotopically enriched FAs may accumulate in the higher trophic level omnivores because of their consumption of a variety of prey items that have fed on iPOM. For example, diet studies of bearded seals and Pacific walrus have determined that an original iPOM FA signature was prominent after the transfer through multiple trophic steps from a diverse benthic prey spectrum (Oxtoby unpublished data). The diet of the snow crab used here as an omnivore representative consists of polychaetes, bivalves, amphipods, and other crustaceans (Kolts et al. 2013; Divine et al. 2015); all these taxa incorporate FAs from the POM sources (e.g., Oxtoby unpublished data), which are then transferred into the snow crab during predation. Notably, in a study of benthic invertebrates from the Bering Sea, polychaetes contained the highest FA $\delta^{13}C$ values (Oxtoby unpublished data). These data could identify the pathway along which relatively high FA $\delta^{13}C$ values are channeled to the omnivorous crab species *Chionoecetes opilio.*

The two biomarker approaches used in this study, FA concentrations and FA $\delta^{13}C$ values, resulted in different patterns for the various feeding types. FA concentrations indicated that subsurface and surface deposit feeders fed most prominently on ice algae while FA isotope values suggested that omnivores consumed the most ice algae. We provide a number of reasons for this discrepancy, such as insufficient source specificity of the FAs (i.e., they may be produced by both ice algae and phytoplankton, or additionally another source altogether) or high variability because of low concentrations of the target FAs. Stable carbon isotope values of FAs resolve at least some of the source specificity issues between ice algae and phytoplankton, and we, therefore, suggest that the FA-specific isotope values are the more suitable biomarker approach to the questions asked here. Hence, the high $\delta^{13}C$ values of the most ice algal-specific FA 16:1(n-7) in omnivores indicate relatively high contribution of iPOM specifically to this feeding type.

Spatial and temporal patterns in iPOM sourcing

The significant difference between feeding types in $\delta^{13}C$ values of 16:1(n-7) prompted us to analyze whether spatial differences may exist in ice-algal use within and among feeding types. Our analysis of environmental influences on FA biomarker patterns did not reveal any strong environmental correlations. Stations were unlikely to be associated with different water masses: all stations in 2012 had salinities >32.2 characteristic for Bering Sea Anadyr Water or Winter Water, except one station close to Wrangel Island that was under some melt water influence (Ershova et al. 2015). The homogeneity in water characteristics may explain why FA $\delta^{13}C$ values in most feeding types (both deposit and suspension feeders) did not show strong spatial trends. However, local nutrient concentrations can still differ even within the same water mass based on levels of drawdown, mineralization and stratification patterns (Tremblay and Gagnon 2009). This may have been important in the spatial patterns found for omnivores, for which 16:1(n-7) was most enriched in ^{13}C at stations near Wrangel Island. The Wrangel Island region is partially influenced by the cold Winter Water exiting through Herald Canyon southeast of Wrangel Island, which is high in nutrients (Woodgate et al. 2005; Pickart et al. 2010; Ershova et al. 2015). This nutrient rich water could cause a large local ice algal bloom and, subsequently, more iPOM production for organisms to feed on. Omnivores may show this increased iPOM production more than the other feeding types in the region if a 'bioaccumulation' effect through preying on other invertebrates (Oxtoby unpublished data) sets them apart from the other feeding types, as discussed above.

Over the span of our sampling period, FA $\delta^{13}C$ values of subsurface deposit feeders, surface deposit feeders and suspension feeders increased slightly. These and other trends were statistically significant but variability was high and trends slight, suggesting that these trends may be of low biological importance. However, this increase in FA isotope values could reflect continued turnover of these FAs when feeding on ice algae over a long time period. This could support the idea of a 'food bank' in polar sediments (Mincks et al. 2005; Glover et al.

2008; Weems et al. 2012), where organic material gets stored in sediments over long time periods (months to years) to provide a continued food source for benthic sediment feeders. This food bank could particularly store ice algae that settle in a matter of days (Haecky et al. 1998; Ambrose et al. 2005) while phytoplankton remains suspended in the water column longer because of stronger currents in the summer before settling (Van der Loeff et al. 2002; Woodgate et al. 2005). Also, a larger portion of phytoplankton feeds into the pelagic food web while most ice algae sink to the seafloor (Hunt et al. 2002; Szymanski and Gradinger 2016). Continued consumption of accumulated iPOM with relatively high $\delta^{13}C$ values, and continued isotopic turnover in the consumer tissues, could isotopically enrich the FA biomarker values over time in consumers. This mechanism could especially explain the increase in FA $\delta^{13}C$ values of subsurface and surface deposit feeders. However, if re-suspension is high, particularly in the shallow waters of the Chukchi Sea (Weingartner et al. 2005; Woodgate et al. 2005), even suspension feeders may utilize 'food bank' materials in some capacity, resulting in a similar increase in $\delta^{13}C$ values over time. It is uncertain why a similar increase over time was not found in omnivores that derive their FA signals mostly from the prey organisms they consume (Oxtoby unpublished data), many of which are suspension or deposit feeders. The slight increase in 16:4(n-1) $\delta^{13}C$ values and decrease in 16:1(n-7) $\delta^{13}C$ values over time could possibly be a result of a diet shift. Omnivores are known to consume a wide variety of prey organisms that can differ over the geographic range (Divine et al. 2015), but little is known about temporal shifts in prey spectra and if this could cause a change in $\delta^{13}C$ values of FAs over time.

Conclusions

All three targeted FAs are produced by diatoms, but our results show that they may not be sufficiently source specific to distinguish between ice algae versus phytoplankton. It seems that bacterial production also may play a larger role than previously thought, especially for 20:5(n-3) and probably also 16:1(n-7), which will need to be elucidated more fully in future studies. Although 16:4(n-1) may be a good biomarker for diatoms, and specifically ice algae, its low concentrations are problematic for its accuracy and subsequent interpretation. We invoke the idea of a food bank in Arctic sediments as a continued source of FAs to consumers, which should be especially available to deposit feeders, as indicated by the high FA concentrations in subsurface deposit feeders. The relatively high $\delta^{13}C$ values in all FAs in omnivores may be a result of this feeding type integrating and accumulating the FA isotope values of their prey organisms, which may source their FAs from iPOM. In summary, this study showed that the prominent benthic feeding types in the Chukchi Sea differ in their use of various carbon sources, but we are in need of more specific biomarkers of sea ice algae if we are to understand the specific implications of the anticipated changes in sea ice production with increased climate warming. One possibility of such a specific biomarker may be the isoprenoid IP_{25} that is suggested to be highly specific to only ice algae and can be traced through consumers (Brown et al. 2014).

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General Conclusion

Arctic benthic ecosystems play a significant role in the uptake and respiration of organic matter reaching the seafloor (Ambrose et al. 1995; Renaud et al. 2008). Both sea-ice algae and marine phytoplankton are currently major primary production sources for Arctic benthic consumers, but climate change-induced loss of sea ice may shift primary production to increasing phytoplankton and reducing ice algal contributions. To investigate the usage of sea-ice algal and phytoplankton carbon in benthic feeding types, I used two biomarker approaches, fatty acid (FA) concentrations as well as FA specific stable carbon isotope analysis. Results indicate that FA specific isotope analysis is likely the more appropriate method for investigating connections between sea ice particulate organic matter (iPOM) and benthic consumers as it seems that FAs alone may not have the necessary level of specificity to distinguish the two primary production sources. Based on FA stable isotope values, I concluded that omnivores, represented by the snow crab *Chionoecetes opilio*, may ingest the largest amounts of iPOM.

Several ecological concepts could explain these results. Strong feeding plasticity in Arctic benthic consumers (Iken et al. 2010) may dilute reliance on a specific food source (e.g., feeding on resuspended material in addition to strictly feeding on freshly sinking material in suspension feeders). Feeding plasticity will also equip benthic consumers to take advantage of organic material contained in sediments, which also allows them to feed during the low-productive winter season (Brown et al. 2015). This concept of a sediment "food bank", originally proposed for Antarctic benthic systems (Mincks et al. 2005), could de-couple benthic consumers from the direct influx and availability of fresh primary production and will likely make them more resilient to changes in timing and even quality of organic matter (e.g., North et al. 2014). Omnivores such as snow crab, which feed on organic matter throughout the sediment depth as well as on prey items that themselves feed on this sedimentary organic matter, could possibly bio-accumulate the ice algal biomarker signal more easily if this source is available year-round.

This study has shown that biomarker approaches to studying the specific use of sea-ice algal production in Arctic benthic consumers still need further research. This may also explain the, at times, contradictory results of investigations of sea ice algal use in Arctic benthic consumers in the literature. For example, different biomarker studies have shown significant and even preferential sea-ice algal use (McMahon et al. 2006, Sun et al. 2009), while Mäkelä et al. (2018) found that phytoplankton carbon is preferentially respired over sea-ice algal carbon by the Arctic benthos. To resolve such contradictions, biomarker approaches for tracking sea ice algae may need to be more carefully applied. The original assumption made in my study that the three target FAs are specific indicators for diatoms and that sea ice algal communities consist mostly of diatoms may need to be re-evaluated. In the future, it may also be helpful to add stable carbon isotope composition of a flagellate FA biomarker, to differentiate the iPOM source better from the phytoplankton POM (pPOM) source. In addition, the presumed

Arctic sea-ice algal specific highly branched isoprenoid IP_{25} could be a useful biomarker for sea-ice algae as shown in some initial Arctic benthic food web studies (Brown and Belt 2012, Brown et al. 2012, 2014).

Table 1 Coordinates of sampled stations with dates of sampling and respective program that sampled the station. Station numbers as in Fig. 1

Sampling Date	Station #	Station ID	Latitude (°N)	Longitude (°W)	Sampling depth (m)	Cruise collected
8/17/12	1	H14	72.42	161.24	46	COMIDA
8/30/12	2	CS4	66.93	170.97	43	RUSALCA
9/5/12	3	CEN3	70.29	176.67	57	RUSALCA
9/6/12	4	CEN1a	70.71	178.31	38	RUSALCA
9/7/12	5	HC3	71.02	175.99	48	RUSALCA
9/7/12	6	HC1	70.71	173.91	40	RUSALCA
9/8/12	7	N02	72.50	166.84	44	Arctic Eis
9/10/12	8	M04	72.00	163.65	35	Arctic Eis
9/12/12	9	K02	71.00	166.97	39	Arctic Eis
9/13/12	10	CL8	67.87	172.55	53	RUSALCA
9/13/12	11	CL10	67.40	173.60	34	RUSALCA
9/13/12	12	M02	72.00	166.88	40	Arctic Eis
9/14/12	13	CS8R	67.43	169.61	51	RUSALCA
9/17/12	14	D02	67.50	167.19	40	Arctic Eis

Table 2 Stable carbon isotope values of the pPOM and iPOM for FAs 16:1(n-7), 16:4(n-1) and 20:5(n-3) for sampling in different years and data accumulated from different sources. Values are given as *means* in ‰ ± 1 *SD*. n/d indicates no data

Source	Year	16:1(n-7)	16:4(n-1)	20:5(n-3)	Data Source
iPOM	2002	n/d	-24.0 ± 2.4	-18.3 ± 2.0	Budge et al. 2008
	2009	-21.0 ± 6.8	n/d	-26.5 ± 3.0	Wang et al. 2014
	2010	-25.2 ± 4.5	n/d	-26.5 ± 2.8	Wang et al. 2014
	2014	-23.1 ± 2.1	n/d	-31.3 ± 0.2	This study
	Average	-23.1 ± 2.1	-24.0 ± 2.4	-25.7 ± 5.4	All studies
pPOM	2002	n/d	-30.7 ± 0.8	-26.9 ± 0.7	Budge et al. 2008
	2009	-28.8 ± 1.5	n/d	-29.7 ± 1.3	Wang et al. 2014
	2010	-28.4 ± 1.2	n/d	-29.7 ± 1.6	Wang et al. 2014
	2010	-29.7 ± 1.7	n/d	-29.3 ± 1.6	Wang et al. 2014
	2010	-29.5 ± 1.6	n/d	-30.2 ± 1.6	Wang et al. 2014
	Average	-29.1 ± 0.6	-30.7 ± 0.8	-29.2 ± 1.3	All studies

Table 3 Overall *ANOVA* results for the comparison of FA concentrations with feeding type for 16:1(n-7), 16:4(n-1) and 20:5(n-3). Values are sum of squares (*SS*), mean squares (*MS*), degrees of freedom (*DF*), test statistics (*F*). * denotes significant differences at $\alpha = 0.05$, which was met at p=0.0083 after *Bonferroni adjustment* of the data

Fatty acid	Factors	*SS*	*MS*	*DF*	*F*	*p*
16:1(n-7)	Feeding type	0.175	0.058	3	6.854	< 0.001*
16:4(n-1)	Feeding type	0.001	$3.417 \bullet 10^{-4}$	3	13.350	< 0.001*
20:5(n-3)	Feeding type	0.003	0.001	3	0.295	0.829

Table 4 *Tukey test with Bonferroni correction* for feeding type comparison for 16:1(n-7) and 16:4(n-1). * denotes significant differences at $\alpha = 0.05$, which was met at $p = 0.0083$ after correction

Fatty acid	Feeding type comparison	*p*
16:1(n-7)	Omnivore vs. Subsurface	< 0.001*
	Omnivore vs. Surface	0.015
	Omnivore vs. Suspension	0.567
	Subsurface vs. Surface	0.718
	Subsurface vs. Suspension	0.032
	Surface vs. Suspension	0.267
16:4(n-1)	Omnivore vs. Subsurface	< 0.001*
	Omnivore vs. Surface	0.068
	Omnivore vs. Suspension	0.487
	Subsurface vs. Surface	0.005*
	Subsurface vs. Suspension	< 0.001*
	Surface vs. Suspension	0.686

Table 5 Overall *ANOVA* results of comparison of FA isotope values with feeding type as factor for 16:1(n-7), 16:4(n-1) and 20:5(n-3). Values are sum of squares (*SS*), mean squares (*MS*), degrees of freedom (*DF*) and test statistics (*F*). * denotes significant differences at $\alpha = 0.05$

Fatty acid	Factors	*SS*	*MS*	*DF*	*F*	*p*
16:1(n-7)	Feeding type	100.500	33.490	3	9.028	< 0.001*
16:4(n-1)	Feeding type	25.050	8.351	3	2.627	0.063
20:5(n-3)	Feeding type	10.700	3.568	3	1.982	0.131

Table 6 *Tukey test with Bonferroni correction* for feeding type comparison for 16:1(n-7). * denotes significant differences at $\alpha = 0.05$, which was met at $p = 0.0083$ after correction

Fatty acid	Feeding type comparison	*p*
16:1(n-7)	Omnivore vs. Subsurface	0.021
	Omnivore vs. Surface	0.002
	Omnivore vs. Suspension	< 0.001*
	Subsurface vs. Surface	0.846
	Subsurface vs. Suspension	0.301
	Surface vs. Suspension	0.764

Table 7 Linear regression analysis between FA stable carbon isotope values and sampling time for all feeding types for 16:1(n-7), 16:4(n-1) and 20:5(n-3). * denotes significant differences at $\alpha = 0.05$

Feeding type	*df*	*m*	R^2	*F*	*p*
		16:1(n-7)			
Omnivore	34	-0.233	0.153	6.131	0.018*
Subsurface	40	0.063	0.082	3.582	0.066
Surface	34	0.064	0.327	16.520	<0.001*
Suspension	39	0.094	0.186	8.880	0.005*
		16:4(n-1)			
Feeding type	*df*	*m*	R^2	*F*	*p*
Omnivore	34	0.174	0.132	5.026	0.032*
Subsurface	40	0.062	0.052	2.190	0.147
Surface	34	0.104	0.142	5.447	0.026*
Suspension	39	-0.075	0.044	1.800	0.188
		20:5(n-3)			
Feeding type	*df*	*m*	R^2	*F*	*p*
Omnivore	34	-0.065	0.085	3.146	0.085
Subsurface	40	0.093	0.459	33.920	<0.001*
Surface	34	0.082	0.264	12.210	0.001*
Suspension	39	0.138	0.231	11.710	0.001*

Table 8 Results of the 2-factor *ANOVA* with feeding type and station as factors for 16:1(n-7). Values are sum of squares (*SS*), mean squares (*MS*), degrees of freedom (*DF*) and test statistics (*F*). * denotes significant differences at $\alpha = 0.05$

Fatty acid	Factors	*SS*	*MS*	*DF*	*F*	*p*
16:1(n-7)	Feeding type	0.723	0.241	3	174.87	< 0.001*
	Station	0.337	0.026	13	18.79	< 0.001*
	Feeding type:Station	0.505	0.017	30	12.22	< 0.001*

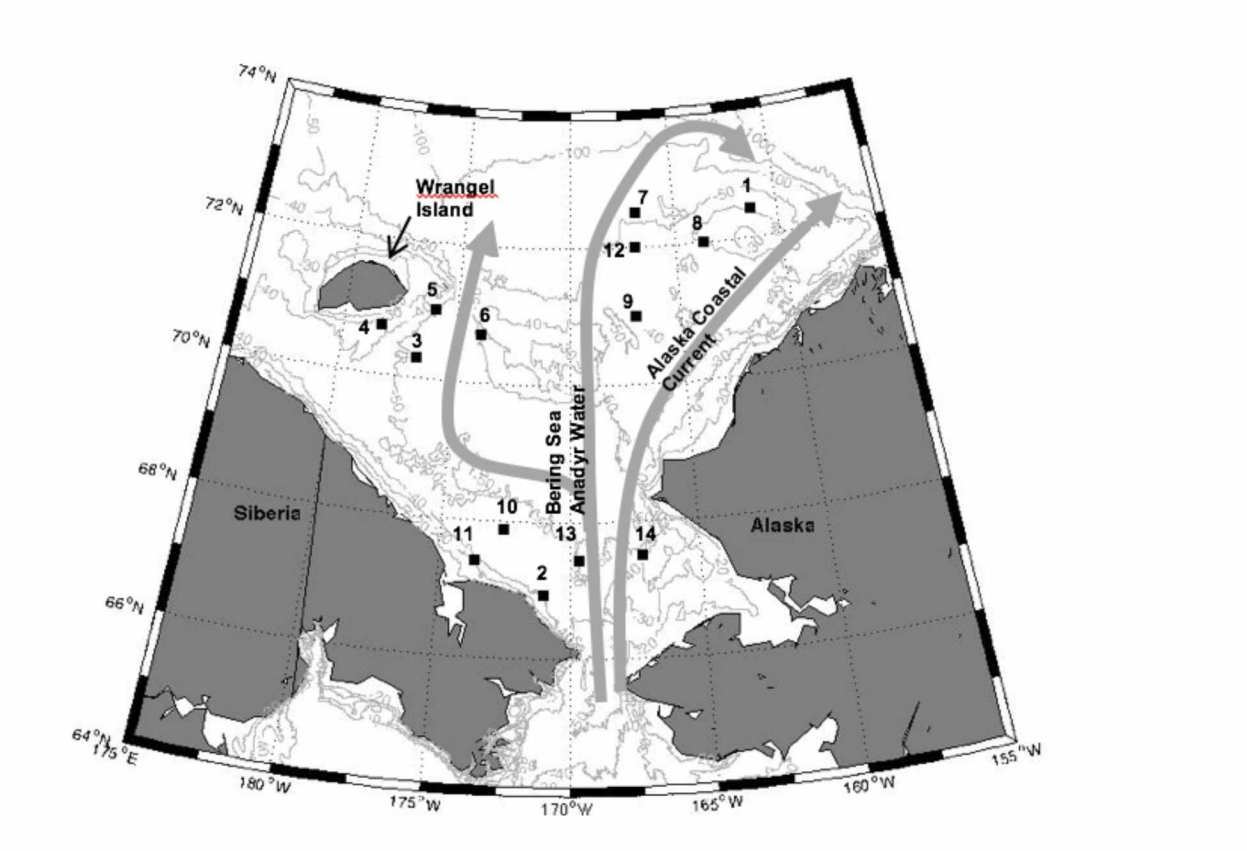

Fig. 1 Sampling stations (referred to by station #, see Table 1) in the Chukchi Sea in August and September 2012 with grey arrows denoting major water masses based on Pickart et al. (2010)

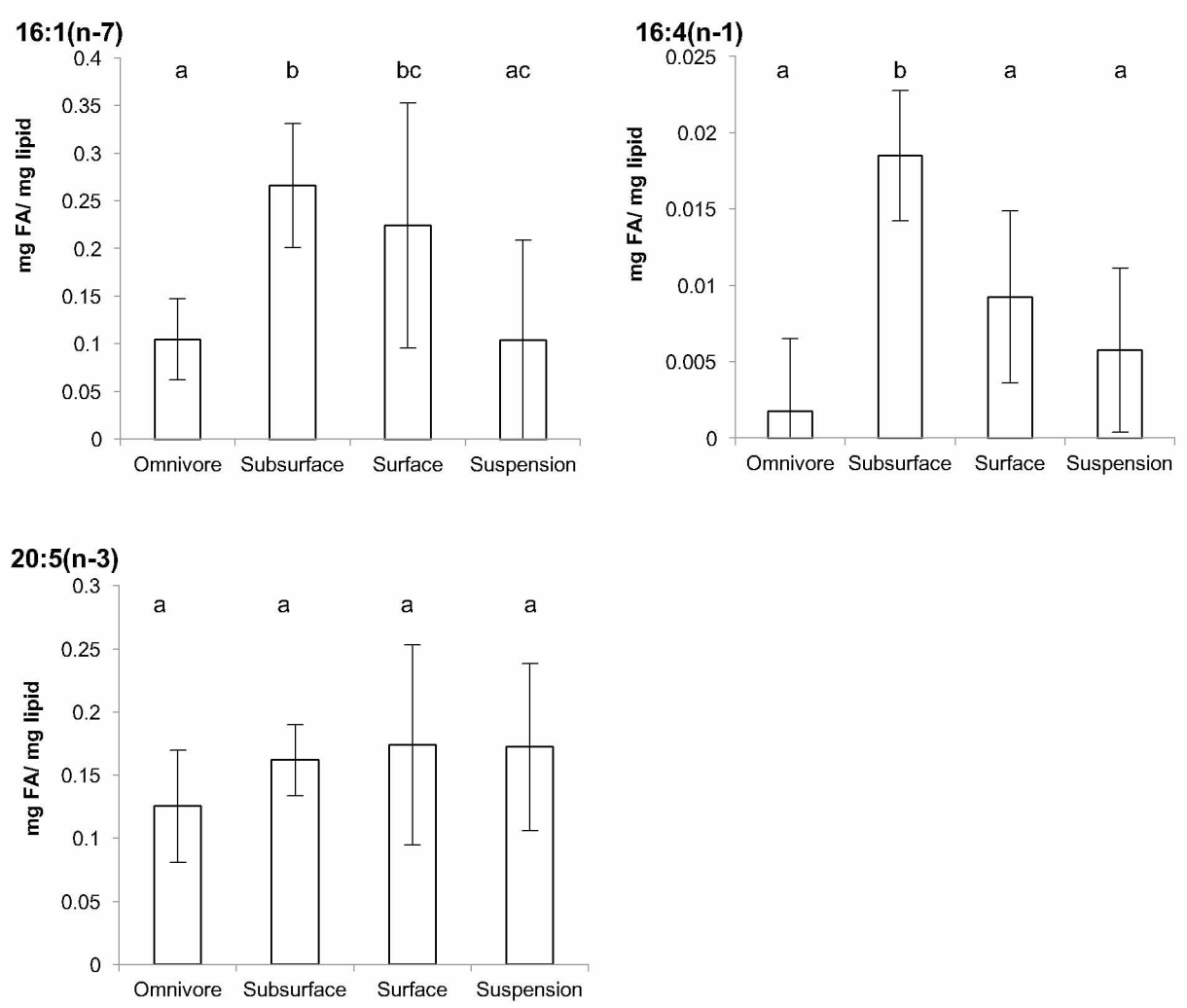

Fig. 2 FA concentrations for the FAs 16:1(n-7), 16:4(n-1) and 20:5(n-3) for different feeding types. Values are given as *means* ± 1 *SD* with different letters above bars denoting significant differences within each FA comparison. Note difference in y-axis scale for FA 16:4(n-1)

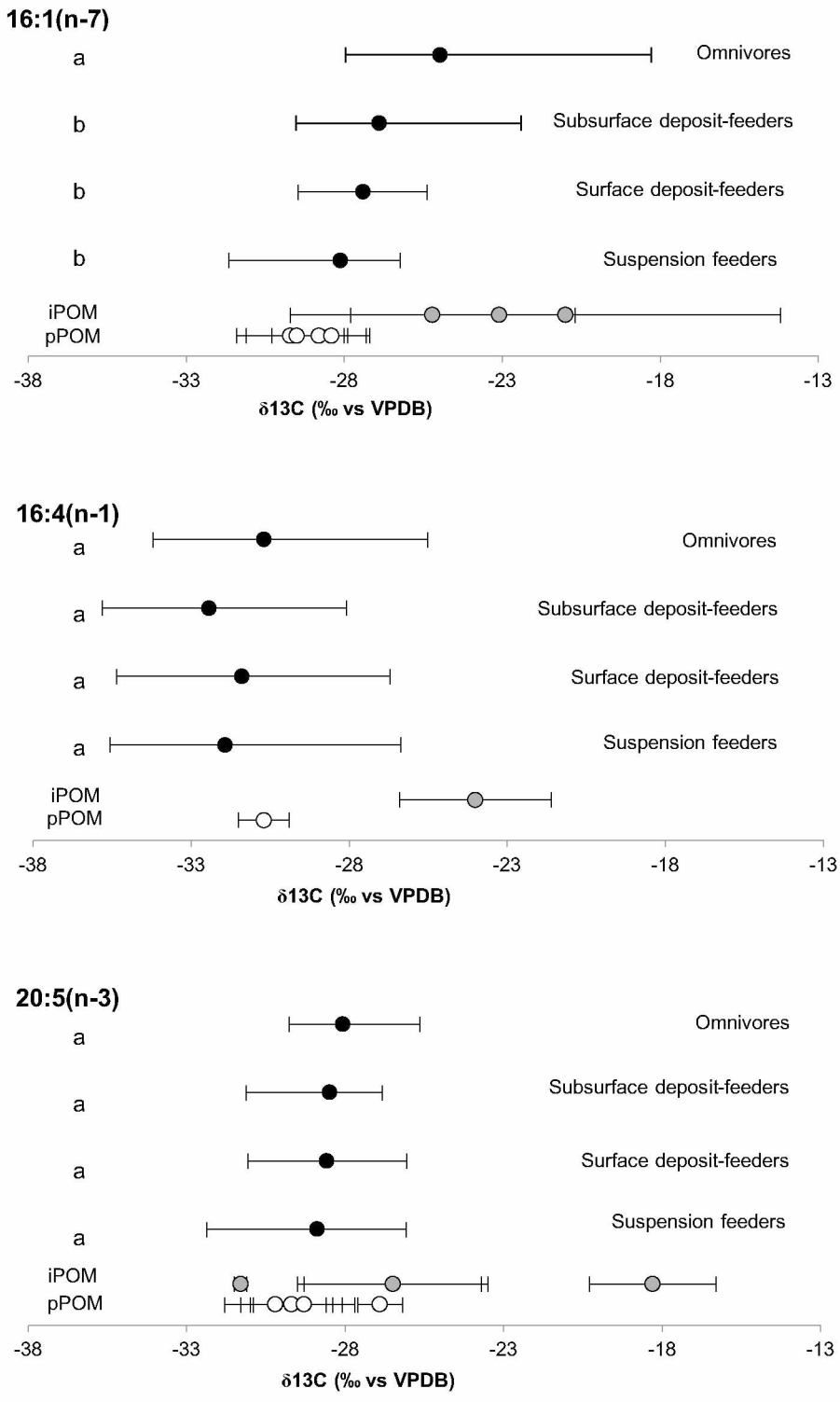

Fig. 3 $\delta^{13}C$ values (*mean* ± *SD*) for 16:1(n-7), 16:4(n-1), and 20:5(n-3) in relation to iPOM and pPOM $\delta^{13}C$ ranges with letters next to *SD* bars denoting significant differences. See Table 2 for iPOM and pPOM value origins

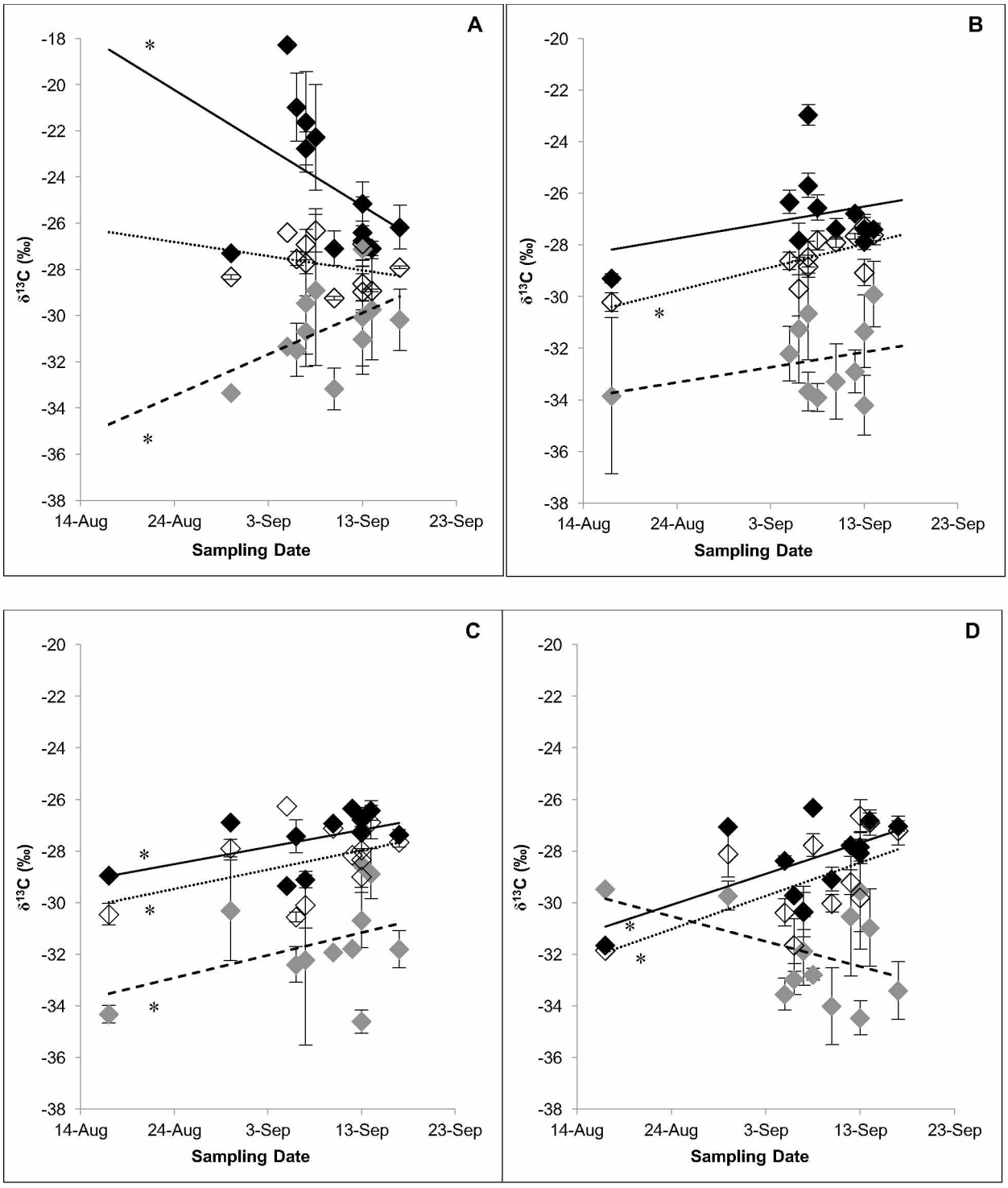

Fig. 4 $\delta^{13}C$ values for omnivores (A), subsurface deposit feeders (B) surface deposit feeders (C) and suspension feeders (D) over sampling time. Symbols represent FAs: 16:1(n-7) (black fill, continuous regression line), 16:4(n-1) (light grey fill, dashed regression line), 20:5(n-3) (no fill, dotted regression line). * denotes significant linear regressions at $\alpha = 0.05$

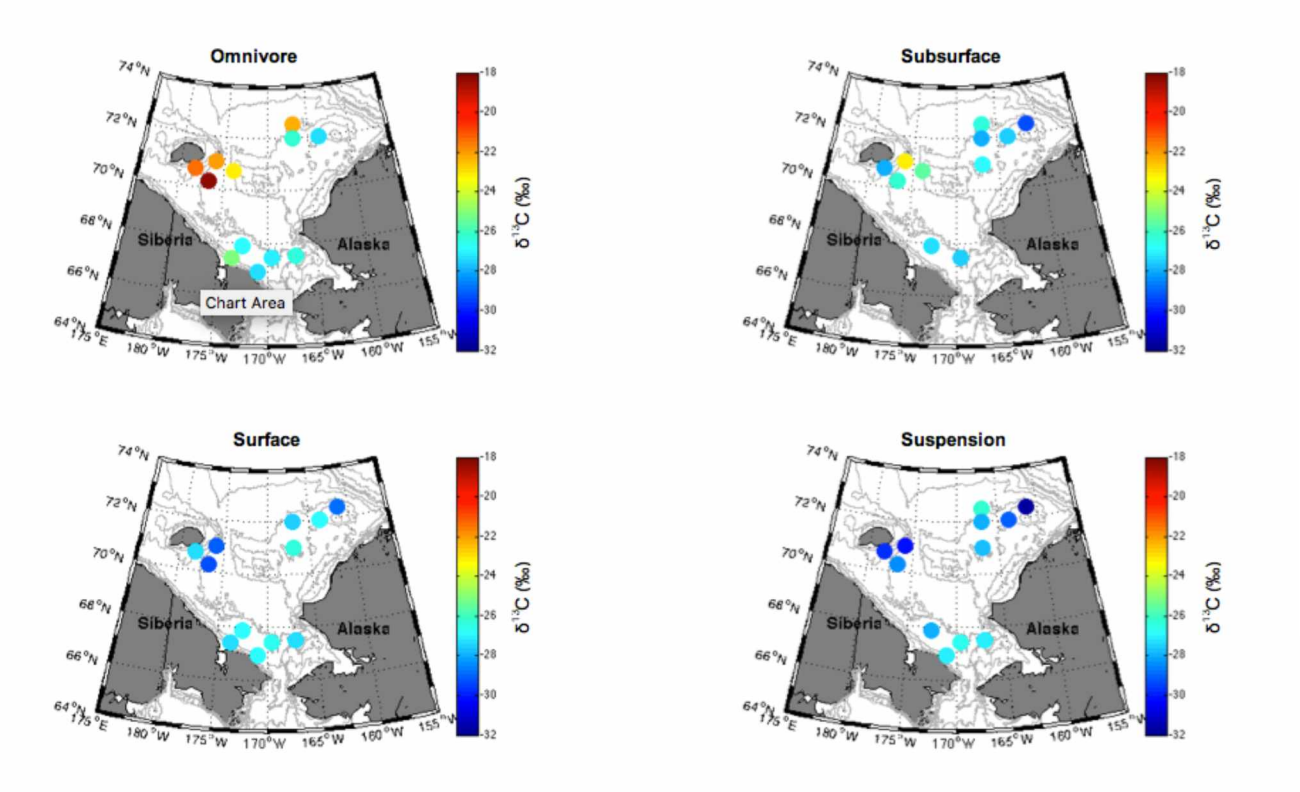

Fig. 5 Spatial distribution of $\delta^{13}C$ values of 16:1(n-7) for all feeding types. Location of Wrangel Island as indicated in Fig.1

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